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Charles A. Ross
Western Washington University, charles.ross@wwu.edu

June R. P. Ross
Western Washington University

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BIOSTRATIGRAPHIC ZONATION OF LATE PALEOZOIC DEPOSITIONAL SEQUENCES

CHARLES A. ROSS[1] AND JUNE R. P. ROSS[2]

1 Chevron U.S.A., Inc., P. O. Box 1635, Houston, TX 77251
2 Department of Biology, Western Washington University, Bellingham, WA 98225

ABSTRACT

Correlation of more than seventy third-order depositional sequences in Carboniferous and Permian strata uses assemblage zones of warm water benthic and nektonic shelf faunas. These include calcareous foraminifers, bryozoans, conodonts, and ammonoids and represent tropical, subtropical, and warm temperate water faunas from carbonate shelves and adjacent cratonic basins.

After the Early Carboniferous faunal zonation was highly provincial and worldwide correlations of depositional sequences are based on interpretations of evolutionary lineages and depositional patterns in each province and in identifying times of limited dispersals between provinces.

Associated with these faunal zones there were times of expanded or reduced faunal diversities and temperature related latitudinal expansion or reduction of faunas. Higher sea levels during warmer times enhanced faunal evolution and diversity and lower sea levels during cooler times dampened evolution and diversity and resulted in many species becoming extinct.

After the Early Carboniferous, provincial faunal zonations and evolutionary lineages developed as a consequence of the formation of Lesser Pangaea. Further isolation of these provinces resulted in faunal realms in the middle Early Permian after the formation of Greater Pangaea.

INTRODUCTION

Establishing the timing of depositional events is critical in analyzing late Paleozoic sea-level fluctuations. Fortunately, a number of fossil groups have been studied in great detail so that most late Paleozoic stratigraphic successions around the world can be correlated with considerable precision. We present in this paper a brief summary of four fossil zonations that are commonly used for correlating late Paleozoic strata and try to evaluate the precision that is available. Two zonations are based on foraminifers and bryozoans which are marine benthic shelf organisms that showed preferences for different depositional environments. The other two zonations are based on cephalopods and conodonts which were nektonic and formed part of the ecosystem in the water column above these marine shelves. The empty shells of cephalopods may float and be carried by currents great distances beyond their habitat. Conodonts are elements from an organism about which we know virtually nothing of its life habits.

The following discussion is centered around the faunal zone columns on the Carboniferous and Permian cycle charts in the accompanying article on 'Late Paleozoic sea levels and depositional sequences' by Ross and Ross (this volume).

PALEOGEOGRAPHIC CHANGES

In order to understand and use late Paleozoic fossil zonations, it is important to keep in mind that changes in paleogeography, in climate and climatic fluctuations, and in ocean currents had great influences on the dispersal, evolution, and extinctions of these faunas (Ross and Ross, 1985a).

The assemblage of Lesser Pangaea at the end of the Early Carboniferous and the assemblage of Greater Pangaea in the middle of the Early Permian increasingly disrupted the tropical, subtropical, and warm temperate marine shelf faunas, giving rise to biogeographical provinces and finally to realms. These geographic changes took place over 100 million years in a series of steps (Figs. 1 to 4) that brought together first Gondwana and Euramerica and later added Angara to form the extremely large landmass Pangaea. Changes in land mass distribution also changed ocean basin shape and size, ocean current dynamics, temperatures, and ultimately changed climates and the distribution of climatic belts. Associated with these geographic changes were tectonic and orogenic events and a northward transport of Pangaea so that its northern marine shelf was moved into cooler and cooler waters. Cool ocean currents were redirected toward the equator along the western marine shelves of Pangaea and consistently westward directed warm equatorial currents flowed along the eastern marine shelves of Pangaea and fostered great faunal diversification in the Tethys region.

Gondwana was the largest of the cratonic blocks and was so large that some of its shelves were commonly within warm temperate and subtropical regions at the same time that other parts were at the southern pole. Euramerica was considerably smaller and was situated across the equator extending into the northern part of the tropical area. The ocean basin and its sediments between Euramerica and Gondwana were in the process of being deformed into the Hercynian-Appalachian-Ouachita-Marathon orogenic

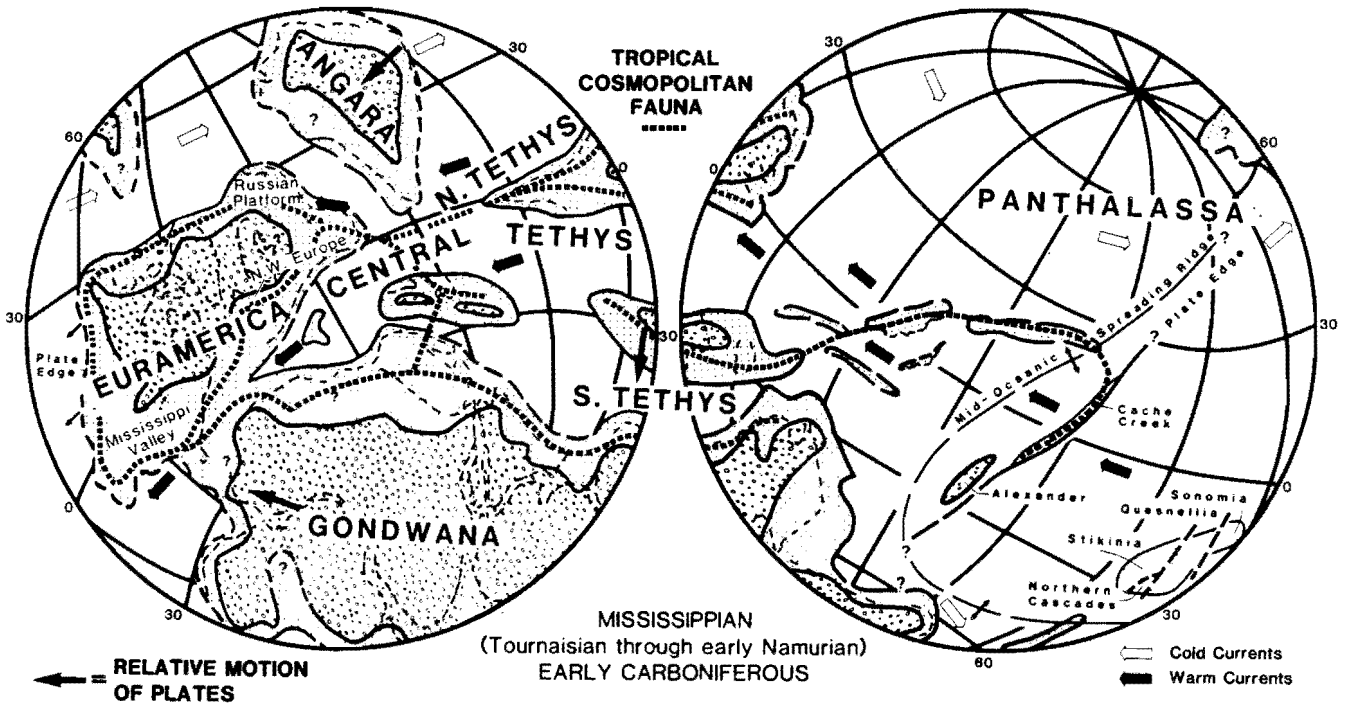

FIGURE 1. Paleogeographic map for the Tournaisian through early Namurian showing relative motions of plates (large black arrows), direction of ocean surface currents (small black arrows = warm currents; small open arrows = cold currents), and shallow shelf areas (stipple). (Revised from Ross and Ross, 1981.)

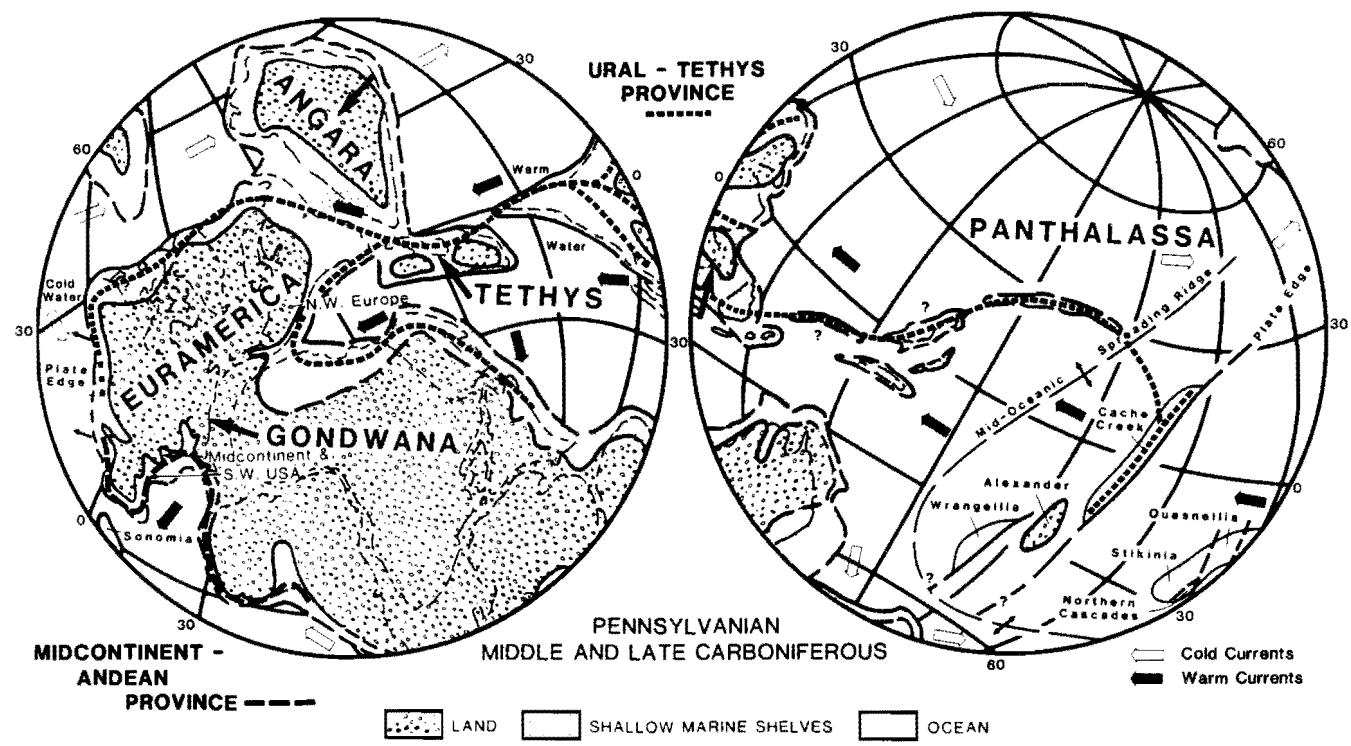

FIGURE 2. Paleogeographic map for the Middle and Upper Carboniferous. Gondwana rotated clockwise against Hercynian - Appalachian - Ouachita - Marathon orogenic belt during this time. (Revised from Ross and Ross, 1981.)

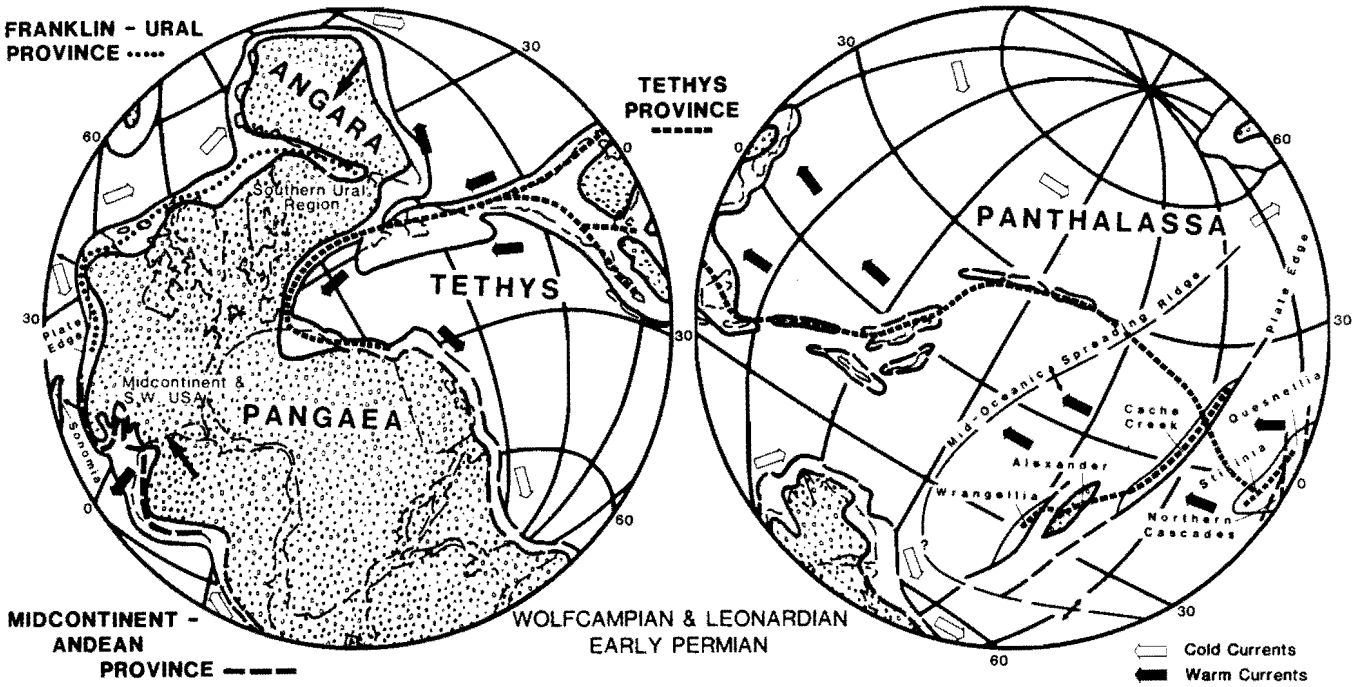

FIGURE 3. Paleogeographic map for the Early Permian shows the separation of the Ural region and Russian Platform from the PaleoTethys which dates from the Middle Leonardian. (Revised from Ross and Ross, 1981.)

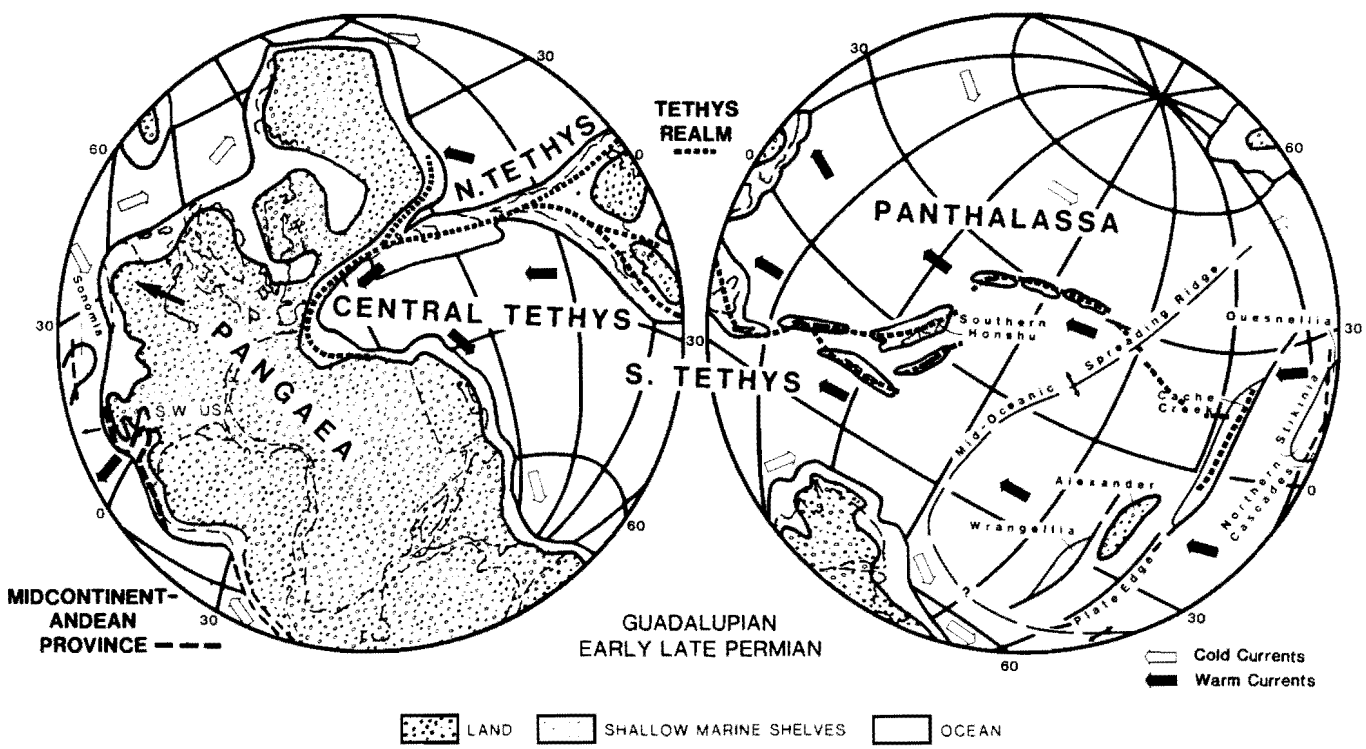

FIGURE 4. Paleogeographic map for the Guadalupian shows the position of Greater Pangaea extending across all the latitudinal climatic belts. (Revised from Ross and Ross, 1981.)

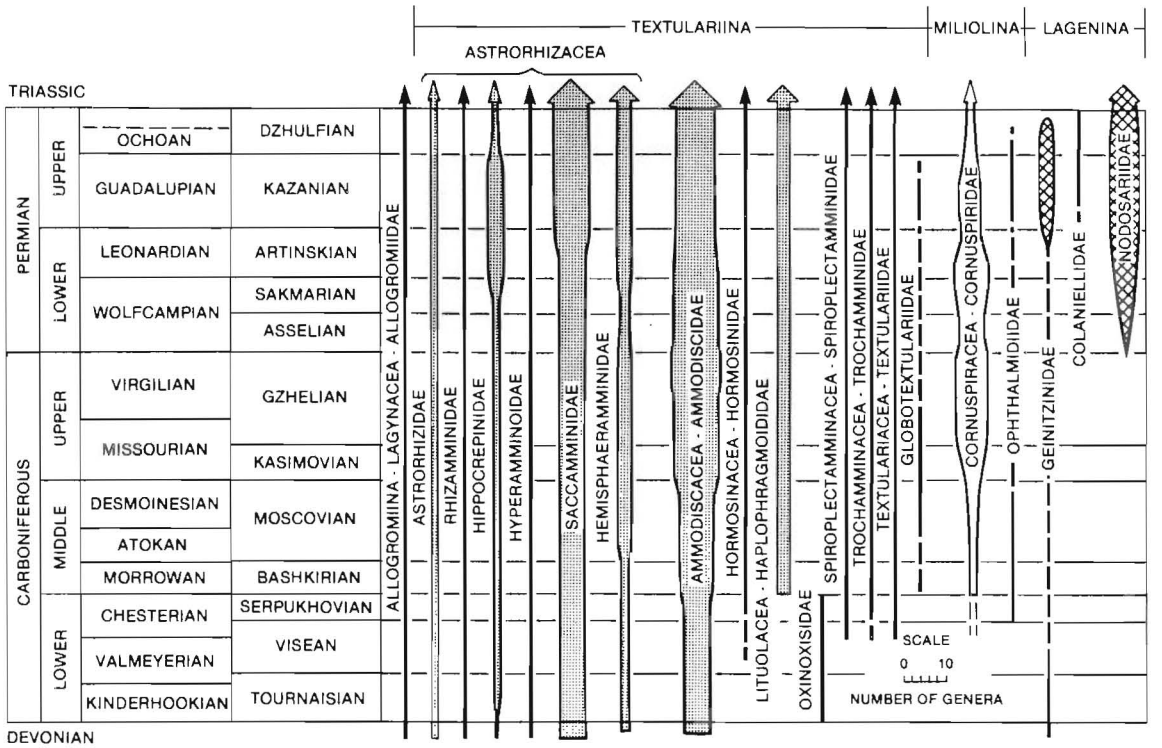

FIGURE 5. Stratigraphic ranges of Paleozoic families of Foraminiferida (data modified from Loeblich and Tappan, 1984).

belt and only the Acadian orogenic phase had been completed by the Early Carboniferous. In the middle portion of the belt, for example in Spain, central France, and the Maritime provinces of eastern Canada, several Armorican and Avalonian microcratons had been accreted to one or the other of the larger cratons during Devonian time.

Angara lay to the north and east of Euramerica in warm to cold temperate to cold latitudes. The Ural ocean basin separated Angara from eastern Euramerica during the Carboniferous.

The geographic position and makeup of the fourth major cratonic block, China, is less well known. It is made of a dozen significant cratons. South China and North China were separate in the Devonian. The Carboniferous faunas and floras are strongly indicative of a warm temperate to subtropical position and, for parts of South China, a tropical position during the Carboniferous and Permian. Western China appears formed of additional large stable blocks. Much about the paleogeographic history of the area remains to be discovered.

Each of these four major cratonic blocks have large areas of relatively undisturbed shelf deposits of late Paleozoic age which include thick carbonates, glacial-marine deposits, phosphatic sandstones, black shales, coals, and fluvial deltas, and data on these, in addition to fossil assemblages, provide the basis to reconstruct the paleogeographic relationships of these cratons with some confidence.

Ocean basins of the late Paleozoic are less known and less understood than the cratons. Active mid-ocean spreading centers during the Mesozoic and Cenozoic caused the accretion of late Paleozoic sea-floor sediments (and also some younger sediments) as structurally deformed margins to the Paleozoic cratons. The stratigraphy and fossils of these accreted margins are less thoroughly studied than those of the craton, and it has been recognized only since the early 1970's that these margins include rocks that have been transported long distances. The world ocean basin, PaleoPanthalassa, had a large western region, PaleoTethys, which contained numerous small island arcs and small to medium size cratons. Our reconstruction of central and eastern PaleoPanthalassa also suggests several oceanic plates (with island arcs and trenches) bounded by subduction zones, similar to those now in the western Pacific.

FAUNAL PROVINCES

Late in the Early Carboniferous (late Visean through Namurian B) Gondwana and Euramerica joined along the Hercynian-Appalachian-Marathon orogenic belt to form Lesser Pangaea. This divided the tropical marine shelf along the southern margin of Euramerica and eliminated the marine connection that had joined the shelf faunas of western Euramerica with those of the eastern PaleoTethys. Because parts of the coast of Gondwana remained near the south pole and in cold water, the two tropical shelf faunas became isolated, one on either side of Lesser Pangaea. Dispersals between them were infrequent along the only available warm temperate route on the northern (Franklinian) shelf of Euramerica.

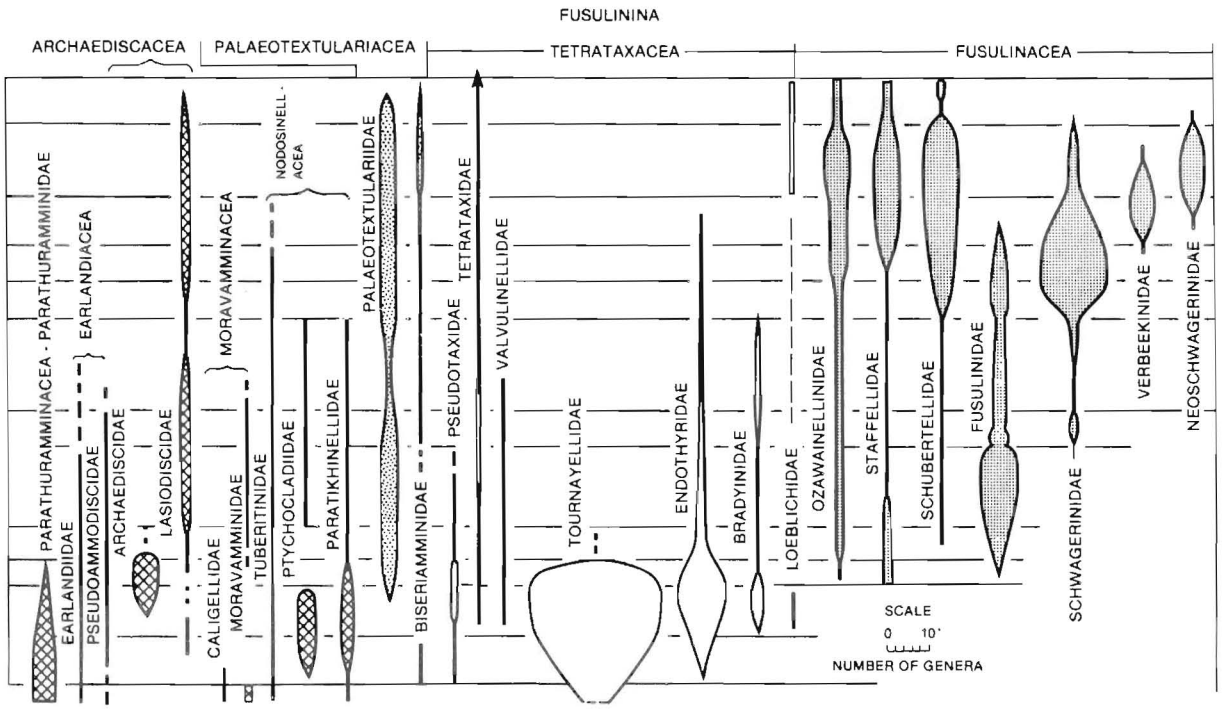

FIGURE 5. (Continued).

Equatorial warm water currents were diverted northward along the Russian Platform and southward along eastern Gondwana into much cooler regions and resulted in increased precipitation and a general climatic cooling. Glaciation in Gondwana resumed during the Early Carboniferous (Namurian) and continued with fluctuations until near the end of Early Permian.

During the Middle and Late Carboniferous and the earliest Early Permian, Lesser Pangaea continued on a northerly track and the north coast of Euramerica was gradually displaced to higher and cooler temperate latitudes. Shelf faunas occasionally dispersed by that route during times of higher sea-levels (which were also times of warmer water temperatures).

Another major geographic change resulted when Lesser Pangaea joined with Angara along the Ural orogenic belt in the middle Early Permian to form Greater Pangaea. Angara was being displaced from the north or northeast and its coasts extended well into cold temperate or boreal waters. By eliminating the currents of warm water from the Tethys area that had been flowing northward through the Ural marine connection, the northern shelf of Euramerica lost its physical connection to the Tethys and became much cooler. Its outpost populations of warm-adapted, shelf shelly faunas diminished greatly after this event.

The marine shelves of Greater Pangaea extended into both the cold northern and southern seas and effectively completed the isolation of the tropical marine shelf faunas on either side of Pangaea. Each fauna evolved independently with only occasional species dispersal by island "hopping" across Paleo-Panthalassa.

The assemblage of Greater Pangaea may have affected world climate by redirecting ocean surface currents into more latitudinally compartmentalized flow. Climates, in general, appear to have gradually warmed during the later Early Permian, suggesting a connection with paleogeographic changes.

FORAMINIFERAL ZONATION

The ranges and abundance of genera in late Paleozoic families of foraminifers are shown in Figure 5. Most of the Textulariina, particularly the Astrorhizacea are made up of conservative, long ranging genera and species. Many of these were common in the outer parts of shelves, on the slopes and in basins in dark fine clastic sediments. Except for the Kinderhookian and pre-Carboniferous strata, the astrorhizaceans are seldom used in correlation, and even in those rocks conodonts are more generally used. The first appearances of the Spiroplectamminidae and Trochamminidae contribute to Lower Carboniferous zonations. The Globotextulariidae is a minor family in the Middle and Upper Carboniferous and extends into the Upper Permian.

Among the calcareous Foraminifera, the first appearances of several genera in the Cornuspiridae are important in outer shelf (or "deeper-water") limestones in the middle and later part of the Lower Carboniferous and into the Lower Permian. Genera and species were long-ranging so that first appearances are used.

In the Lagenina, three families make their first appearance in the late Paleozoic. The Geinitzinidae and Colaniellidae are restricted to Upper Paleozoic beds and the Nodosariidae, which begin in the Early Permian, extend into the Mesozoic and Cenozoic. These are warm water families and the Nodosariidae, although common in darker gray basinal limestones, may have been transported there from other habitats.

The Fusulinina superfamilies Archaediscacea, Palaeotextulariacea, Tetrataxacea, and Fusulinacea had the most rapid diversification and have been the basis for most foraminiferal zonal schemes. These superfamilies were adapted to warm (tropical to subtropical), shallow water, carbonate environments and commonly were prolific. Some may have been host to photosymbionts. For Lower Carboniferous zones, genera and families of the Archaediscidea, Tetrataxacea, and primitive Fusulinacea are most useful.

Foraminiferal zonation of Mississippian carbonates was initially developed in the 1950's and 1960's for the Russian Platform, Ural, and Donetz Basin areas and later extended to other parts of the Soviet Union and has been summarized by Aisenverg (1964), Aisenverg and others (1968), Bogush and Juferev (1966), Brazhnikova and others (1967), Brazhnikova and Vdovenko (1973), Einor (1973), Ganelina (1956), Grozdilova (1966), Grozdilova and Lebedeva (1961), Lipina (1964, 1973), Lipina and Reitlinger (1971), Malakhova and Chuvaschov (1973), Vdovenko (1961) and many others. This scheme is based on identification of characteristic assemblages of species which form biozones.

In northwestern Europe the zonation of calcareous foraminifers in the type areas of the Tournaisian and Visean, was worked out by Conil and Lys (1964, 1973 and in Paproth and others, 1983), Mamet (see summary Mamet,1977), and others. Mamet (1976) and Mamet and Skipp (1971) carried this zonation into the Cordillera region of western Canada and the United States (see also Skipp, 1969; Sando and others, 1969). Because in the Mississippian these areas were parts of the same large tropical faunal province as the Russian Platform, Donetz Basin, and South China, the Tournaisian and Visean foraminiferal zones are widespread and readily recognized. Mamet's early emphasis was on abundances (acme zones), sudden appearances, and evolutionary bursts of species in these shallow water, carbonate faunas. These differences in abundances may represent ecologically widespread features in northwestern Europe, however, other paleontologists in other parts of the world, particularly in the type area of the Mississippian (in the Upper Mississippi Valley) have found difficulty in using these zones as they were originally defined.

Mamet (1977) in summarizing his zonal scheme pointed out that the PaleoTethys during the Tournaisian and Visean had greater diversity than the nonTethys areas and that the foraminifers show paleolatitudinal diversity gradients. Although the key index fossils bridge these latitudinal gradients, the dispersal of many of the genera, particularly among the Bradyinidae and Palaeotextulariidae, to different parts of the PaleoTethys and to other shelf areas was in a heterochronic series of steps. Mamet (1977) suggested that island arcs in PaleoPanthalassa (that now form accreted terranes of the western Cordillera of North America), which have a mixture of species normally endemic to either the PaleoTethys or cratonic North America, served to integrate "regionally distinct biostratigraphic systems." Because phylogenetic faunal sequences are most complete in the PaleoTethys, Mamet (1977) believed most lineages originated there and later dispersed to other areas in an irregular pattern of abrupt first appearances without obvious endemic ancestors.

Baxter and others (1979), Baxter and Brenckle (1982), Brenckle and others (1982) have identified many of the foraminiferal assemblages from the region of the type Mississippian Subsystem. The Gilmore City Limestone and Humbolt Oolite of northcentral Iowa contains middle and late Tournaisian assemblages similar to those of the North American Cordilleran area and are not comparable to those of the Mississippi Valley sections. Scattered lower Visean foraminifers, such as Priscella gp. prisca and primitive Tetrataxis, occur in the Lower Keokuk Limestone. The upper part of the Keokuk also includes Eoendothyranopsis, primitive Globoendothyra gp. tomiliensis and the algae Koninckopora tenuiramosa and are suggestive middle Visean age.

Late middle Visean foraminifers appear in the Salem Limestone and include Archaediscus, Nodosarchaediscus, Globoendothyra baileyi, and continuations of primitive forms of Eoendothyranopsis and Globoendothyra.

The lower part of the St. Louis Limestone (below the breccia beds) has Eoendothyranopsis gp. ermakiensis, rare Eostaffella and complex-walled Septabrunsiina. First occurrences of Archaediscus angulatus, calcitornellids and calcivertellids are in the upper St. Louis. Baxter and others (1979) consider this an assemblage from the lower and middle part of the upper Visean. Ste. Genevieve foraminifers include the stellate archaediscids Neoarchaediscus and Asteroarchaediscus and Endostaffella discoidea. Hemiarchaediscus? is added to this assemblage in the lower Chesterian. This assemblage is of late, late Visean age ($V_{3\varepsilon}$). Endostaffella discoidea disappears in the Glen Dean Limestone and its place in the upper Glen Dean is taken by primitive millerellid-like "Millerella" tortula and "M." designata and by Eostaffella.

The Menard Limestone sees the introduction of eosigmoilinids represented by the first appearance of Brenckleina rugosa and Eosigmoilina robertsoni. The highest Chesterian foraminiferal assemblage is from the Kinkaid Limestone and contains "Millerella" cooperi and small, primitive true Millerella.

Baxter and Brenckle (1982) place the Visean-Namurian boundary at the base of the

Menard Limestone, a position that most others would consider too high. We have retained a more traditional correlation and placed it one cycle lower just above the Glen Dean Limestone at the base of the Cypress Sandstone. Rich (1980, 1986) has established a useful foraminiferal zonation for Chesterian strata in the Black Warrior basin of northern Georgia and Alabama.

As with other shallow shelf faunas, foraminifers were greatly reduced in diversity by the end of the Chesterian and there was a brief time when only the Archaediscidae were abundant. Although a number of genera and most families did survive into the Middle Carboniferous, their importance in carbonate-producing communities was replaced by new genera and families in the Fusulinacea.

The Middle Carboniferous to Late Permian foraminiferal zonations are based on a succession of genera and species of fusulinaceans (Dalmatskaya and others, 1961; Douglass, 1977; Dunbar and Skinner, 1937; Kalmykova, 1967; Kanmera and others, 1976; Kotljar and Stephanov, 1984; Leven, 1967; Leven and Shcherbovich, 1978; Ozawa, 1970; Ross 1967; Rozovskaya, 1975; Sheng, 1963; Skinner and Wilde, 1965; Thompson, 1964; Toriyama, 1967; and many others). A few of the lowest Middle Carboniferous zonal fossils are species that had ancestors in the upper Visean and lower Namurian (e.g., Eostaffella, Millerella, and Pseudoendothyra). The Morrowan foraminifers lack forms that were elongated along the axis of coiling.

The overlying Atokan had the beginnings of several very successful lineages. Species of Profusulinella followed rapidly by species of Fusulinella formed the nucleus of some shallow shelf, ecologically stable communities. These two genera persisted through the Middle Carboniferous in the Russian Platform and PaleoTethys. However, in Midcontinent North America, these same two genera had short stratigraphic ranges that only just overlapped and Fusulinella gave rise to Beedeina and Wedekindellina with only minor range overlap in the lower part of the Desmoinesian. In addition, on the Russian Platform Fusulinella gave rise to Fusulina (s.s.) which briefly was common there, but which was virtually unknown in the North American Midcontinent. The Russian Platform also has a number of genera which are known from the PaleoTethys, but not from the Midcontinent, for example Eofusulina, Verella, Hemifusulina, and Aljutovella.

The highest two or three depositional sequence in the Middle Carboniferous show a decrease in fusulinacean diversity and the highest Middle Carboniferous sequence in the Midcontinent appears to lack fusulinaceans. In the PaleoTethys and the Russian Platform, these cycles had a few new genera that appearred briefly, such as Putrella, Pseudotriticites, and early species of Quasifusulinoides and were forerunners of Late Carboniferous fusulinaceans.

The nearly complete replacement of Middle Carboniferous fusulinacean genera by new genera in the Late Carboniferous is well documented by Rozovskaya (1975) for the Soviet Union and by Thompson (1957) and Thompson and others (1956) for the Midcontinent area of North America. Some of these new fusulinids may be widespread, but this is largely concealed by the use of different generic names in the Midcontinent of North America and in the Russian platform. For example, the lineage at the base of the Upper Carboniferous of the Russian Platform and Ural region called Fusulinella by Soviet paleontologists is probably represented by Eowaeringella in the Midcontinent area; Protriticites from lower Upper Carboniferous beds of the Russian Platform and Ural region is remarkably similar to Kansanella (Iowanella) from the same stratigraphic interval in the Midcontinent. Also from the lower beds of the Upper Carboniferous on the Russian Platform, Quasifusulinoides has the same characteristics as Fusulina fallensis from the lower part of the Missourian of the Midcontinent region. Slighty higher Obsoletes obsoletes from the Russian Platform and Ural region is transitional to the genus Triticites in the same way that the lowest occurrences of Triticites ohioensis in the Midcontinent area are transitional with well developed species of Triticites.

In the middle part of the Upper Carboniferous (Upper Missourian - Lower Virgilian) in most parts of the world, well developed zones are based on similar stages of species evolution within the genus Triticites. Although different faunal provinces existed, the endemic lineages were not as dominant in the fusulinacean communities as those having more cosmopolitan phylogenies and more frequent dispersals.

In the middle and upper Virgilian and Bursum, this situation changed, faunas became much more endemic, and the endemic species dominated most fusulinacean communities in both provinces. Genera such as Daixina, Rauserites, Rugosofusulina, Quasifusulina, and Fusulinella were common and widespread from the Franklinian shelf (northern Canada) through the Ural region and into the PaleoTethys. In the Midcontinent region, Dunbarinella, Leptotriticites and several endemic species lineages of large thick-walled Triticites dominated. Three representatives of Franklinian shelf and Ural region faunas appear briefly in the Midcontinent and southwestern North American regions; first, Waeringella in the middle Virgilian, and then Pseudofusulinella and Rugosofusulina in uppermost Virgilian, Bursum and early Wolfcampian strata. The first two were dispersed from the Franklinian shelf and derived from the long lineages of Fusulinella that were common there during this time. Rugosofusulina dispersed from the Russian Platform.

Foraminiferal zonation of the Lower Permian is complicated by a rapid increase in the number of genera, a continuation of provincial distributions, and a reduction in the dispersal events between geographic distant areas. Two periods of rapid fusulinacean evolution in the Lower Permian

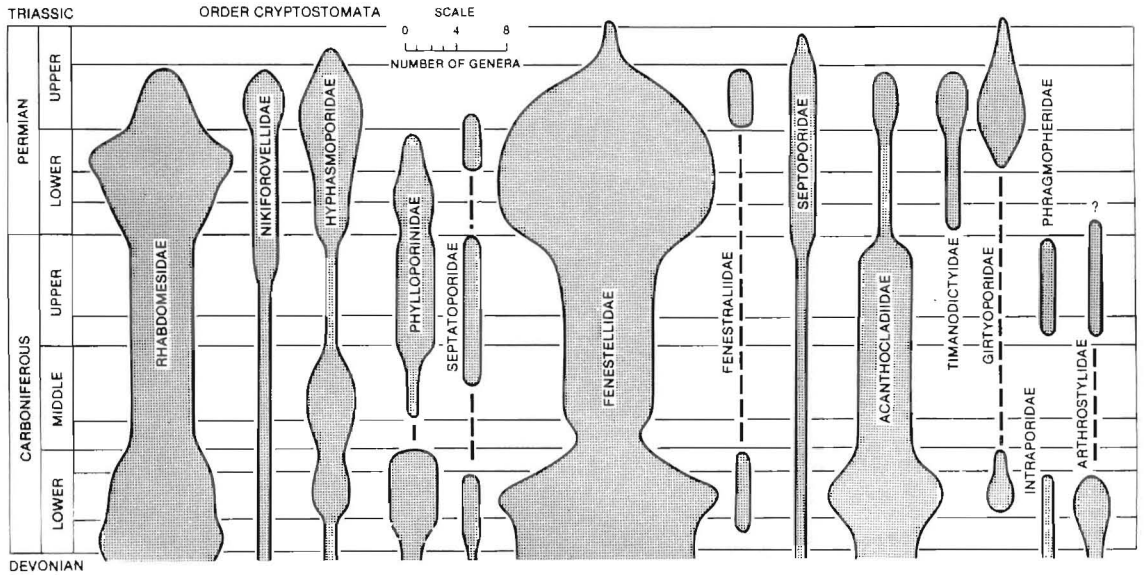

FIGURE 6A. Stratigraphic ranges of Paleozoic families of bryozoans in the order Cryptostomata (after Ross, 1981).

aided zonation. The earliest involved the Schwagerinidae which gave rise to such diverse genera as the subcylindrical Eoparafusulina and Monodiexodina and the subspherical (possibly planktonic or nektonic genera) Pseudoschwagerina, Paraschwagerina, Occidentoschwagerina, Sphaeroschwagerina, Zellia, and Robustoschwagerina, as well as a great number of other genera including Pseudofusulina and Parafusulina. Species of Schwagerinidae form most of the zonal fossils for the Lower Permian. Although some of these may be associated with reef flanks, most lived in less agitated shallow water.

About the middle of the Early Permian, the PaleoTethys region became faunally isolated from the Ural region and a second period of rapid evolution occurred, this time mainly in the Staffellidae and its descendants, the Verbeekinidae and Neoschwagerinidae. These formed a rapid succession of specific and generic zones in the PaleoTethys along with rapid evolution of endemic species in genera of Schwagerinidae. The Neoschwagerinidae were associated with wave agitated reefal features. The Verbeekinidae and Schwagerinidae lived in less strongly agitated environments. Species of Staffellidae were usually in the shallow shelf shallow lagoonal facies. These facies-related PaleoTethyan faunas are made even more difficult to study because later tectonic events commonly have structurally disturbed the facies and stratigraphic relationships.

Upper Permian fusulinacean zones are divided into those of Guadalupian age and those that are younger (Djulfian or latest Permian). Guadalupian zones are based on ranges of species of Parafusulina, Skinnerina, and Polydiexodina in the Midcontinent and southwestern North America realm and on ranges of genera and species of the Neoschwagerinidae, Verbeekinidae, Staffellidae, and Schubertellidae in the PaleoTethyan faunal realm. Ozawa (1970) devised a particularly useful species lineage zonation for some of the Neoschwagerinidae in southeast Asia starting with Misellina minor and leading to Lepidolina kumaensis. Near the end of Guadalupian, most large fusulinaceans became extinct. Lepidolina kumaensis was apparently the last survivor and occurs in strata considered earliest Djulfian by Japanese geologists.

Only the Staffellidae and relatively small Schubertellidae and Ozawainellidae survived through the Djulfian during which time a number of new genera evolved. At the species level, the Djulfian may be subdivided into zones using Paleofusulina and Codonofusiella. These fusulinid faunas are part of the PaleoTethyan faunal province and are not well distributed even within that realm. Other foraminifers, including species of Colaniella, Lasiodiscus, Abadehella, Pachyphloia, Nodosaria, and Paraglobivalvulina, are used to supplement this zonation in parts of the PaleoTethyan realm (Ishii and others, 1975; Okimura and others, 1985). None of the fusulinaceans range into Triassic strata. The cause of the extinction of most fusulinid families near the end of the Guadalupian and their final extinction at the end of the Djulfian remains unknown.

BRYOZOAN ZONATION

The stratigraphic distribution of bryozoan families for the late Paleozoic is shown in Figure 6 A, B. The extinction and evolution of genera are illustrated by the width of the outline of the family ranges. At the level of families, bryozoans demonstrate a large diversity of forms in the Tournaisian and a slightly larger diversity in the early and middle Visean (Ross, 1981a, b; 1984). This speciation was followed by a rapid, progressive decline in diversity late in the Visean through the Serpukhovian and into the Bashkirian. The Moscovian shows only a slight

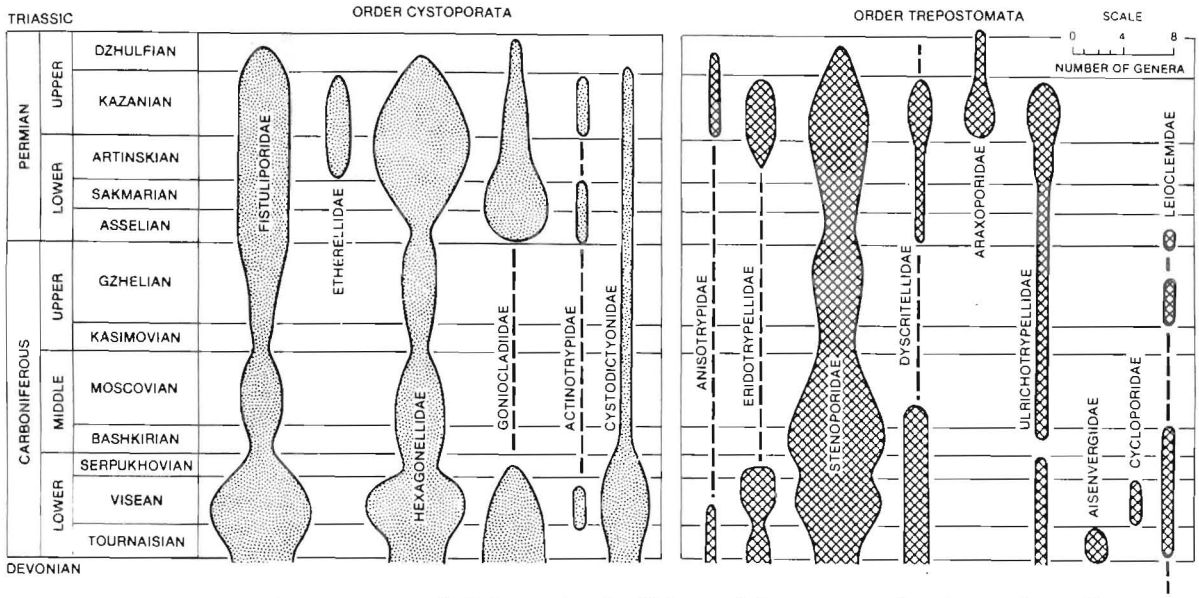

FIGURE 6B. Stratigraphic ranges of Paleozoic families of bryozoans in the orders Cystoporata and Trepostomata (after Ross, 1981).

increase in diversity and near the end of that stage shows another decline in several families. The Upper Carboniferous had a fairly stable, if somewhat low, diversity.

Beginning in the Asselian, new genera were gradually added to a number of families, particular to the Hexagonellidae, Goniocladiiae, Rhabdomesidae, Hyphasmoporidae, and Fenestellidae (Ross, 1978, 1979). A few families having only one or two genera in the Lower Carboniferous, such as the Actinotrypidae, Anisotrypidae, Eridotrypellidae, Fenestraliidae, Girtyoporidae, and others, are not known from strata of Middle or Upper Carboniferous ages and presumably survived in paleogeographic refuges that are not known at present. Genera of these families start to reappear in the Asselian and this repopulation is completed by the beginning of the Guadalupian (= Kazanian). Accompanying these Early Permian reoccurrences are a few new and distinctive families, the Timanodictyidae, Etherellidae, and Araxoporidae.

The Guadalupian (Kazanian) bryozoans show a change in faunal dominance as more and more genera of Rhabdomesidae and Fenestellidae became extinct. All the other bryozoan families declined in diversity and abundance during the Guadalupian and only nine families survived into the lower part of the latest Permian (Djulfian) and of those only four into the upper part. Only a few Djulfian genera survived into the early Triassic before becoming extinct.

These patterns of family level diversity are of interest because they reflect change that occurred at the same times as those seen in the second-order cycle sea-level curve and also many of the changes in diversity seen in other groups of marine organisms.

Studies of the stratigraphic ranges and paleogeographic distribution of individual genera (Ross, 1978, 1979, 1981, 1984 and Ross and Ross, 1981) illustrate that genera commonly have significantly different stratigraphic ranges in different faunal provinces and that the times of dispersals from one area to another are more frequent than just at the beginning or end of a particular stage. For example, there were three or four times of dispersal during the Visean and these may relate to four sea-level highstands (see Lower Carboniferous Cycle Chart, this volume). The Middle and Late Carboniferous data show similar frequent dispersal patterns. In the Permian, there are three obvious times of changes in paleogeographic dispersals, one within the lower part of the Artinskian, another at the end of the Artinskian (or perhaps the Ufimian) and the third at the end of the Guadalupian. These few episodes of dispersals suggest that Permian bryozoan were less influenced by third-order sea-level changes in their dispersals than their Carboniferous ancestors.

Detailed studies of bryozoan species distributions in closely controlled stratigraphic successions aid in identifying different depositional sequences. Trizna (1958) in her study of Lower Carboniferous bryozoans of the Kuznets Basin (Fig. 7) found six assemblages which differed in species associations and in species abundances. Although Trizna's data does not have detailed bed by bed distributions, we have reconstructed such a distribution using stratigraphic and faunal data from Selyatitsky and others (1975). The Lower Carboniferous of the Kuznets Basin includes many sandstones, evaporites, tuffs, and dolostones. There also are widespread fossiliferous Tournaisian limestones and, in the northwestern part of the basin, some fossiliferous Visean limestones. As with the Moscow basin, the succession has numerous unconformities that separate non-fossiliferous and some fossiliferous sequences. Using reported foraminiferal data, we have assigned the bryozoan assemblages to the Russian

Platform and northwest Europe depositional sequences.

CONODONTS

Conodonts occur in a great variety of lithologies that represent many contrasting depositional environments and indicate that they were nektonic (Seddon and Sweet, 1971). Shallow water deposits typically have less diversity of conodont elements than deeper water deposits, and in some parts of the Paleozoic succession, an approximate depth zonation of conodont-bearing organisms is possible (Merrill, 1972, 1975).

Conodont zonations for the late Paleozoic, as with most other biostratigraphic zonations, have regional differences which probably relate to environmental and geographical separation. Conodonts show these regional differences less distinctly than some other faunal groups. They are widely used for correlating parts of the Carboniferous and Permian where they are extremely valuable.

The conodont zones of the latest Devonian and earliest Mississippian (Kinderhookian) are known in remarkable detail. In western North America, Sandberg (in Sando, 1985a) has worked out a scheme based on the first occurrences of species of Siphonodella, Gnathodus, Scaliognathodus and Dolignathodus from the later part of the Devonian to about the middle of the Visean. The remainder of the Lower Carboniferous is based on assemblage zones utilizing a number species of Cavusgnathus and Hindeodus, Taphrognathus varians, Gnathodus girtyi, Adetognathus unicornis and Rachistognathus muricatus. Although many of these assemblages are known from Europe, they are not represented well in the Mississippian type area where a generally similar set of assemblage zones using different species and some different genera is used (Collinson and others, 1971).

The Kinderhookian part of the conodont zonation is particularly detailed in that it adds three zones below the first widely traceable foraminiferal zone. The middle Visean through lower Namurian part of the conodont zonation becomes less detailed and the Mississippi Valley and Arkansas sections have more provincial faunas than earlier ones.

Early Pennsylvanian Morrowan zones again show a pattern of assemblage zones of short duration. Lane and others (1971) and Dunn (1974) and Lane and Straka (1974) generally agree on the ranges of most genera and species, however, they use quite different zonal units for the upper part of the Morrowan. As with the detailed zones near the base of the Tournaisian, these conodont zones are considerably more detailed for the Morrowan than are foraminiferal zones.

Atokan, Desmoinesian, and Upper Carboniferous conodont zones have been reviewed by Merrill (1972, 1975). These assemblage zones have species with considerable overlap in species morphologies and require large numbers of specimens to be usable. Permian conodonts are more diverse. Clark and Behnken (1971, 1979) and Behnken (1975) studied their ranges in some detail from both the Great Basin area of the western United States and from west Texas. Kozur (1978) examined conodont zones in the Permian of Europe. Sweet (1970) determined a number of upper Permian zones below the base of the Triassic in the PaleoTethys area. Wang and Wang (1981) were able to apply part of these two sets of ranges to a study of Chinese Permian conodonts and established preliminary zones. The Permian conodont zonation shown on the cycle chart is a compilation of this data. It is not complete and many zonal boundaries are likely to be moved as additional occurrences fill in the ranges.

The Nealian (= Neal Ranch age beds) at the base of the Lower Permian has a conodont assemblage that contains many Late Carboniferous holdovers. The Lenox Hills age beds (Lenoxian) has the additional species Sweetognathus merrilli. In the Leonardian, a number of new species appear in fairly rapid succession to form the basis for a preliminary zonation. Neostreptognathus, Gnathodus, and Merrillina contribute most of the guide species to those zones that are younger than Leonardian.

CEPHALOPODS

Ammonoid cephalopods were one of the first groups to be used for a detailed subdivision of the Carboniferous (see summaries by Paproth and others, 1983; Ramsbottom and Saunders, 1984; Miller and Furnish, 1958; Ruzhentsev, 1960, 1962; Saunders and others, 1979) and Permian (see summaries by Chao, 1965; Furnish, 1973; Miller and Furnish, 1940; Smith, 1929). They show very rapid evolutionary changes that are placed in well defined lineages. Their nektonic habitats were apparently depth partitioned because deeper water lithofacies tend to have increasingly diverse faunas. In contrast to the conodonts, which also show evidence of depth stratification, empty shells of ammonoids floated well and were commonly distributed great distances from their actual habitat range. Because of the shell's propensity to float after the death of the animal, many empty shells were deposited as wind and current flotsam on beaches in death assemblages representing mixed communities (or depth) faunas. In addition, ammonoids are a relatively common fossil (usually compressed) in black shales in environments of slow deposition. They are also known in some "deeper" water carbonate debris and turbidite beds, but as scattered individuals.

Ammonoids show less provincialism than some of the benthic carbonate shelf faunas, probably as a result of their nektonic habitats by which some genera occupied deeper, more widely distributed cooler temperature water masses. Those ammonoids that display the greatest provinciality, such as the Perrinidea, likely were adapted to warm surface waters and had temperature restrictions on their dispersals. Distribution

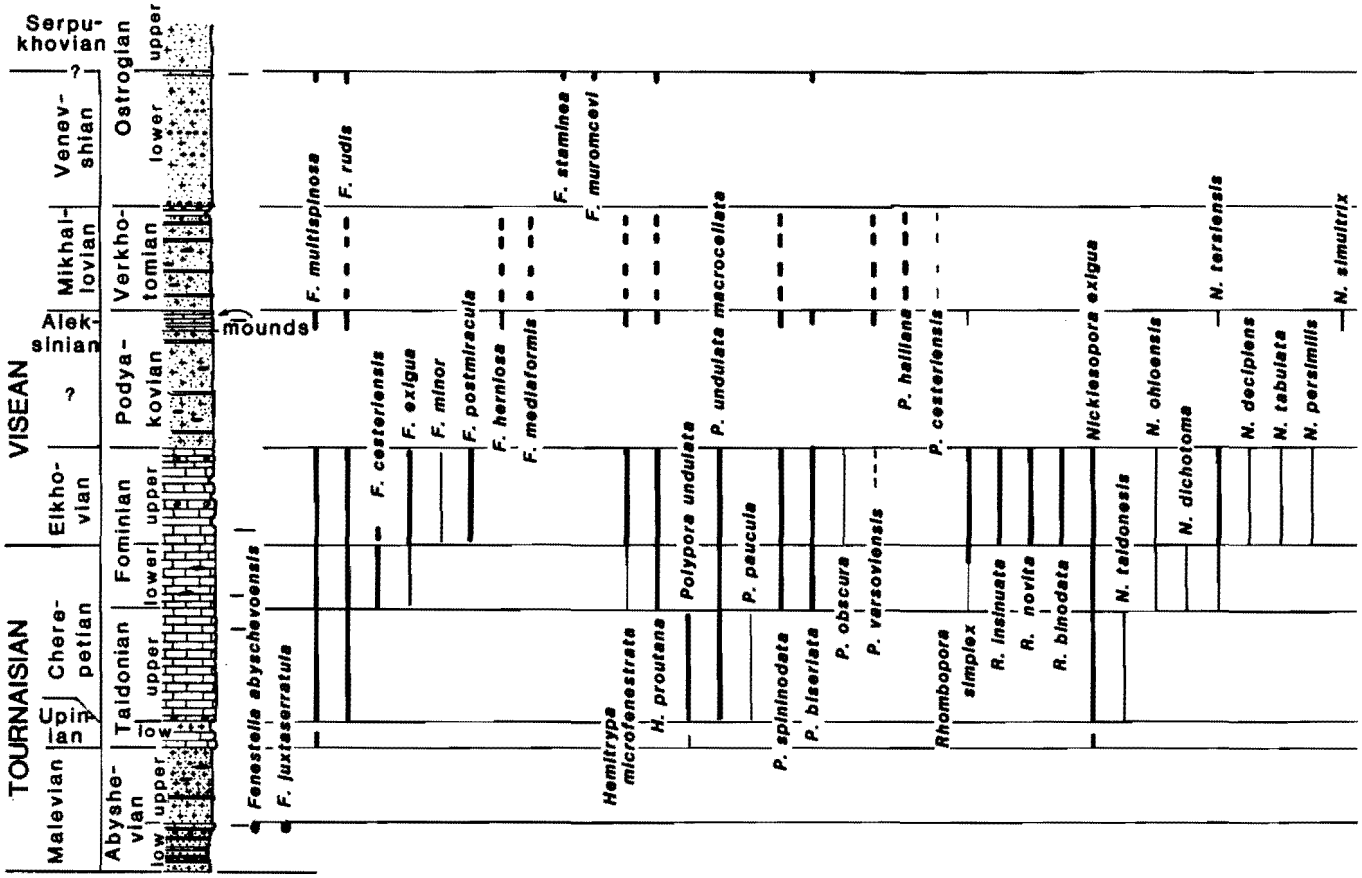

FIGURE 7. Distribution of some bryozoan species and genera in the Lower Carboniferous of the Kuznets Basin, U.S.S.R., (data from Trizna, 1958, and Selyatitsky and others, 1975).

of genera in other families, such as Rectuloceras, suggest random or fortuitous dispersals were common at certain times in the Carboniferous and Permian.

As in most other faunal groups, ammonoids show expansions and reductions in their diversities and geographical ranges. The most obvious is the one at the base of the mid-Carboniferous boundary (Saunders and Ramsbottom, 1986) which may be the result of the effects of greatly lowered ocean temperatures or the result of diminished food supply because ammonoids were predators relatively high in the ecosystem food pyramid.

Ammonoid zonations were the basis for subdividing the Belgium Tournaisian, Visean, and Silesian (Namurian and Westphalian) strata into zones (Paproth and others, 1983), based on species of Muensteroceras, Beyrichoceratoides, Goniatites and related genera. In the lower Namurian, species of Eumorphoceras, Cravenoceras, Cravenocertoides, and Nuculoceras form the typical zonal scheme. The species zones of Homoceras in the Chokierian and Alportian form the basal Middle Carboniferous zones and are not widely distributed outside of northwestern Europe. These zones are equivalent to the lower part of the Morrowan. Upper Morrowan zones include species assemblages of Retites, Recticuloceras, Hudsonoceras, Verneultites, Baschkirites, Bannerоceras, Gastrioceras, and others.

In North America, Atokan, Desmoinesian, and late Carboniferous cephalopods (Böse, 1919; Unklesbay, 1954; Miller and Furnish, 1958) are more common than in northwestern Europe where a generally impoverished fauna is associated with a few thin marine bands. The Midcontinent cephalopods are common in Missourian strata and occur as high as the lower part of the Wabaunsee of the Virgilian. They are not known in younger strata in that area because of unfavorable facies. Strata of Middle and Upper Carboniferous ages on the Russian Platform contain some genera, but few species, in common with those of the Midcontinent and southwestern North America (Ruzhentsev, 1960, 1965).

Permian cephalopod zones were summarized by Furnish (1973). Although Furnish attempted to define or redefine time-stratigraphic stages to be the direct equivalent of cephalopod zones in that article, his discussion of the actual cephalopod zones showed that twelve well-defined assemblage zones can be recognized based on the distribution and stratigraphic ranges of genera in thirty-one families. Furnish (1973) also showed that these families are not evenly distributed geographically. Asselian, Tastubian, Sterlitamakian, and Aktastinian (Wolfcampian to middle Leonardian on the cycle charts used here) have more widely distributed assemblages than do higher Leonardian and Upper Permian cephalopod

assemblages. Only in the middle part of the Leonardian and again in the lower part of the Guadalupian were Paleo-Tethyan and southwestern North America cephalopod families closely associated into biogeographical units.

The Asselian saw the introduction of new genera and families, such as the Metalegoceratidae, Paragastriceratidae, and Popanoceratidae. In southwestern North America the provincial Perrinitidae first appear either just below or in lower Wolfcampian strata (Furnish, 1973). Properrinites and Akmilleri appear in the Upper Wolfcampian Lenox Hills Formation.

Lower Leonardian (Tazlarovian) cephalopods include Metalegoceras, Eothinites, and lower Baigendzhinian cephalopods have Paragastrioceras and Uraloceras in eastern Europe. In southwestern North America species of Medlicottia, Metalegoceras, Popanoceras, and Metaperrinites are widespread in lower Leonardian beds.

The Cathedralian (upper Leonardian) (Ross, 1986) contains distinctive species of Medlicottia, Eumedlicottia, Pseudohalorites, Neocrimites, Almites, and Perrinites, many of which also appear in Coahuila (Mexico), western Guatemala, Timor, arctic Canada, South China, Pamir, and Darvas.

The Roadian contains species of Eumedlicottia, Perrinites, Glassoceras, and others. One locality also contains Texoceras, Peritrochia, and Paraceltites. These assemblages are known mainly in western and northern North America.

The Wordian has a large number of species and genera of cephalopods, particularly common are species of Agathiceras, Popanoceras, Stacheoceras, Waagenoceras, Pseudogastrioceras, and others. Similar species are known from Sicily and Timor.

The upper Guadalupian (Capitanian) is characterized by several species of Timorites. The highest of these assemblages is known only in abundance from Timor (Furnish's, 1973, 'Amarassian Stage') where species of Strigogoniatites, Epadrianites, Stacheoceras, Timorites, primitive Cyclolobus, Hyattoceras, Sundaites, Syrdenites, Episageceras, and Xenodiscus are reported.

The highest Permian Series, the Djulfian includes three cephalopod zones (Furnish, 1973). The lower one has Araxoceras, Vescotoceras, Prototoceras, Pseudogastrioceras and Cyclolobus. The succeeding zone has Vedioceras and species of Cyclolobus, Dzhulfoceras, and longer ranging genera. The youngest assemblage has a diversity of heavily ribbed xenodiscids (Chao, 1965) as well as longer ranging forms. Phisonites triangulus is present in the lower part of this zone and Paratirolites kitti in the upper part and separate the zone into two subzones.

BRACHIOPODS, BLASTOIDS, AND CORALS

Three groups, the brachiopods, blastoids, and corals, have been used for many provincial correlations and, to a lesser extent, for interprovincial correlations. Of these, the brachiopods have abundant provincial faunas which show some dispersals between provinces during the Carboniferous. As with most benthic groups, brachiopods show tropical cosmopolitan distributions during the Tournaisian and early and middle Visean. By the late Visean and early Namurian, decreases in diversities and geographical restrictions becomes apparent. Middle and Upper Carboniferous and Early Permian distributions are very provincial with only a few common genera between even tropical provinces. The Ural-Franklin province is united by having a common brachiopod fauna at this time. During the Guadalupian, southwestern North America and the PaleoTethys had quite different brachiopod faunas. Relatively little consideration has been given to the dispersal history of brachiopod genera or the timing of dispersals. Grunt and Dmitriev (1973) examined some aspects of Permian dispersals in the Soviet Union, however, the overall subject remains not well studied or understood.

Corals also are a group that have good provincial zonation (Federowski, 1981). In the Lower Carboniferous Vaughan (1915) and Hill (1948; 1957) described a good coral zonation for the Tournaisian and Visean (Dinatian) of northwestern Europe. Sando (1985a) and Sando and Bamber (1984) have detailed coral zonation for rocks of similar age in the western margin of the North American craton during the Mississippian. The Middle and Upper Pennsylvanian coral zonation in North America has been summarized by Sando (1985b).

The Lower Permian corals were divided by Minato and Kato (1965a, b; 1971) into two coral provinces, one dominated by waagenophyllid corals, the other by durhaminid corals. Stevens (1982, 1983) and Wilson (1982) have extended studies of colonial Early Permian corals to various parts of western North America. Hill (1958) used coral distributions to help examine Sakmarian geography.

Blastoids in the Chesterian of the type region of the Mississippian show a remarkable species succession (Waters and others, 1985) which seems to be a useful provincial zonation. This group was not widely distributed outside of that province during the Mississippian and was not again abundant until the Permian, and then only in Timor.

DISCUSSION

From the preceding discussions of different fossil groups, it is possible to generalize many of the ecological and environmental conditions at different times during the late Paleozoic.

Changes in the geographic configuration of cratons during the late Paleozoic were sequential. Each major step in this sequence resulted in changes in ocean surface currents, in their temperatures, and in their directions. These, in turn, resulted in changes in world climates as shown by expansion and reduction in glaciation, particularly in Gondwana, in reduction and expansion of carbonate production, fluctuations in sea level, and in the dispersal, extinction, and evolutionary patters of warm water shelf faunas.

The rapid evolution (and subsequent zonation) of the shelf faunas is associated with depositional sequences and may be related to physical changes in the environment, such as temperature, and to the repeated flooding of shallow shelves which encouraged community diversification and specialization. Certainly the adaptive opportunities were greatly increased at these times of sea-level highstands. The subsequent lowering of sea level and restriction of shelf areas may have caused ecosystem disorder and the extinction of some species.

The Tournaisian and most of the Visean were relatively warm and during sea-level highstands had many diverse carbonate-producing communities. Sea level fluctuations were of low magnitude with relatively long frequences. In most of the Tournaisian and Visean, general sea levels were high and the shift of shorelines remained on the shelves. Dispersals were very common with nearly cosmopolitan faunas having latitudinal gradients.

Late in the Visean and in the Serpukhovian (Chesterian), world temperatures cooled rapidly and remained cool during the Bashkirian. Shelf faunal diversity became very low as a result of many extinctions. Surviving genera and families commonly contained only a few species. Carbonate production was generally minor except for a relative narrow equatorial belt. Sea level was generally low. Sea-level fluctuations, however, were of considerable magnitude and of relatively short frequency. Dispersal of benthic shelf faunas was poor. Yasamanov's(1981) studies of Ca/Mg (Fig. 8) suggested the decline in diversity in the later part of the Lower Carboniferous was related to a lowering of surface water temperatures and the gradual increase in diversity during the Early Permian was related to a gradual warming trend.

The Moscovian was slightly warmer than the Bashkirian and, although there was minor faunal diversification, many of the surviving Lower Carboniferous genera became extinct by the end of this stage. Conservative, low diversity shelf communities were the rule, faunal dispersals were irregular and probably fortuitous. Although general sea level rose, sea-level fluctuations continued to be of large magnitudes and of short frequencies.

Late Carboniferous and earliest Permian were times of gradual warming, few extinctions and modest diversification. Dispersals were only slightly more common than during the Moscovian.

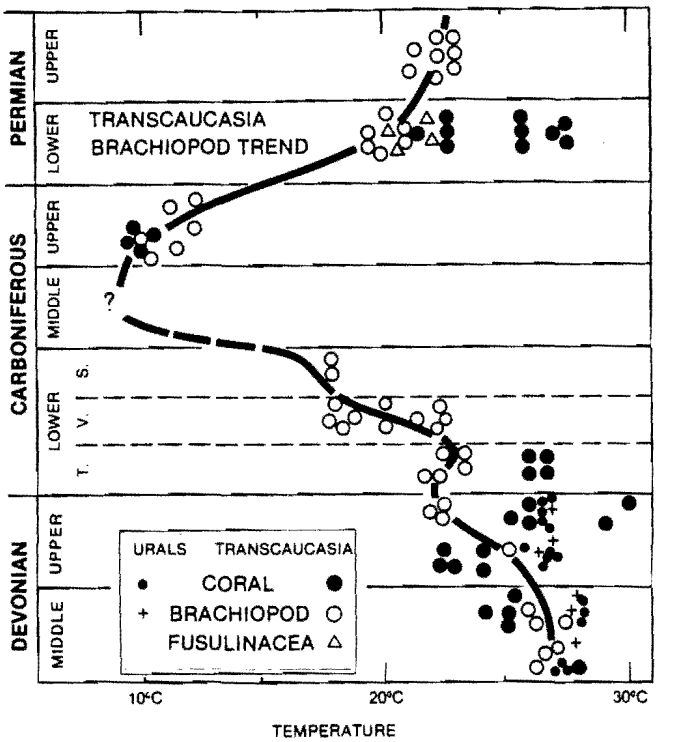

FIGURE 8. A temperature curve for the Devonian through Permian derived from Ca/Mg ratios in corals, brachiopods, and fusulinids (redrawn from Yasamanov, 1981).

The low diversity carbonate mud-bank and mound communities of the Late Carboniferous gradually expanded into somewhat more complex biohermal communities during the earliest Permian. Sea-level fluctuations continued to have short frequencies and large magnitudes.

Later Early Permian (Leonardian) was warm, perhaps as warm as the Tournaisian, and the shelf carbonate faunas show marked diversification. Reef-forming communities gradually evolved independently on both tropical shores of Pangaea. This pattern continued into Guadalupian. Dispersals were extremely rare across Paleo-Panthalassa giving rise to strongly provincial faunas, which were further emphasized in the Guadalupian by increased faunal diversity, particularly in the PaleoTethys. During the later part of the Guadalupian, extinctions again became increasingly common. Although many families had a few surviving genera, they were composed of only a few species. Sea-level fluctuations in the Leonardian and Guadalupian became longer in duration and less in magnitude.

The latest Permian (Djulfian) saw a burst of diversity in the Tethyan faunal realm, which produced some distinctive and briefly successful lineages. These, and the few remaining survivors of the Guadalupian, suffered extensive extinctions before the end of the Permian. The stratigraphic records suggests four rapid sea-level fluctuations of relatively small magnitude which were superimposed on a general lowering of sea level. The shelf faunas in the Tethys include genera and species that may have

been adapted to warm, perhaps very warm water, however, in many other parts of the world, it is difficult to find any faunas or strata that can be identified as being of latest Permian (Djulfian) age.

CONCLUSIONS

Late Paleozoic sea-level fluctuations on the scale of 1 to 3 million years are identified worldwide by specific and generic range zones of many invertebrate groups. Although geographic provinciality was common in the Carboniferous and Early Permian, dispersals of some species and genera took place infrequently.

The resulting fossil zone assemblages are provincial species and genera having independent evolutions and stratigraphic ranges in different provinces combined and mixed with more cosmopolitan (or at least more widely dispersed) species and genera which tie the correlations between different provincial zones together. This type of zonation is dependent upon infrequent dispersals of a relatively small number of species during usually brief times that were favorable for the dispersals. These were apparently warmer times having high sea levels.

Changes in the configuration of continents during the Carboniferous to form Lesser Pangaea and in the middle Early Permian to form Greater Pangaea changed the pattern of oceanic surface currents and progressively isolated the tropical shelves on either side of the supercontinent. Although the Tethys portion of the huge single world ocean, Paleo-Panthalassa, contained many microplates, dispersals of warm water faunas eastward across the main part of the ocean was difficult because of a westward flow of equatorial currents (Ross and Ross, 1981).

The zonation of the Carboniferous and Permian into about seventy warm-water shelf faunal zones is possible and permits the identification of individual third-order sea-level fluctuations worldwide. In part, these sea-level fluctuations themselves may be one of the main contributing causes of the rapid evolution that aids in the zonation. In their role as stratigraphic markers, the recognition of these depositional sequences along with their faunas offers a different and useful approach by which to add more precision to the correlation of late Paleozoic strata.

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